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Fluctuations in defended prey availability modulate the functional response curves of *Menochilus sexmaculatus* (Coleoptera: Coccinellidae)

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Abstract: 【Aim】 In the present study, we assessed the functional response of the 4th instar larvae of a coccinellid species, *Menochilus sexmaculatus* (Fabricius) on aphid species, *Aphis craccivora* Koch and *Lipaphis erysimi* (Kaltenbach) under prey fluctuating conditions. *L. erysimi* is a defended prey that contains allyl isothiocyanates. We hypothesized that under experimental prey conditions, larvae reared on optimal/abundant prey would show better functional response than scarce prey reared larvae. But the slope of the functional response curves would be lower on *L. erysimi* than on *A. craccivora*. 【Methods】 The 4th instar larvae of *M. sexmaculatus* were abruptly shifted from their rearing conditions (*viz.* scarce/optimal/abundant prey) to different experimental conditions (*i. e.*, extremely scarce/scarce/sub-optimal/optimal/abundant prey) and their functional response curves were extrapolated. 【Results】 The results revealed that despite prey resource fluctuations, the 4th instar larvae of *M. sexmaculatus* exhibited the type-II response on *A. craccivora*, but a modified type-II response on *L. erysimi*. Further, irrespective of prey species, the 4th instar larvae that were reared on optimal/abundant prey exhibited normal predation rates under five experimental conditions. But, the 4th instar larvae reared on scarce prey compensated for a shortage of food by consuming higher prey biomass than usual when suddenly switched over to the optimal/abundant prey experimental conditions. However, they exhibited the highest prey consumption on abundant prey and the lowest on extremely scarce prey experimental conditions. Moreover, higher attack rate but lower prey handling time on *A. craccivora* were recorded. 【Conclusion】 Our results suggest that fluctuations in the availability of *L. erysimi* may modify the functional response curves of *M. sexmaculatus* larvae. However, *A. craccivora* is more suitable as a prey for *M. sexmaculatus* than *L. erysimi*.

Key words: Ladybird; aphid; biocontrol; functional response; resource fluctuation

1 INTRODUCTION

Coccinellids (Coleoptera: Coccinellidae) are an important group of predatory insects that are employed as biocontrol agents against aphids and other insect pests (Hodek and Honek, 1996; Michaud, 2012). They have a wide prey range, are very voracious and exhibit rapid functional and numerical responses (Hodek and Honek, 1996; Bayoumy and Michaud, 2012). However, they are best at exploiting aphids and grow better when feeding on aphids than on non-aphid prey (Pettersson *et al.*, 2005; Evans, 2008). While, abundance of aphids in agroecosystems fluctuates in space and time, their availability severely affects life attributes of coccinellids (Santos-Cividanes *et al.*, 2011). As a result, predatory responses of coccinellids differ depending on fluctuations in aphid prey availability (Chaudhary *et al.*, 2016).

The most informative way to study predatory response of coccinellids towards prey resource fluctuations is to measure their functional response to prey abundance or scarcity and correlate it with the biocontrol efficiency of predators (Fathipour *et al.*, 2006; Bayoumy, 2011a, 2011b; Bayoumy and Michaud, 2012; Omkar and Kumar, 2013). There are five types of functional responses, *viz.* Type-I, which is linear (Holling, 1959); Type-II, which is curvilinear (Holling, 1959); Type-III, which is sigmoidal (Holling, 1959); Type-IV, which is dome shaped (Luck, 1985) and Type-V, which is negatively exponential (Watt, 1959). However, type-II functional response predominates in coccinellids (*e.g.*, Omkar and Pervez, 2011; Osman and Bayoumy, 2011; Gupta *et al.*, 2012). Moreover, some studies have also reported modified type-II (Kumar *et al.*, 2014; Chaudhary *et al.*, 2015) and type-III responses in coccinellids (Sarmento *et al.*, 2007; Abdollahi *et al.*, 2010; Bayoumy, 2011a).

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Several studies have earlier evaluated the functional responses of coccinellids, both individually (Sarmento *et al*., 2007; Abdollahi *et al*., 2010; Bayoumy, 2011a; Osman and Bayoumy, 2011; Gupta *et al*., 2012; Omkar and Kumar, 2013) and within combinations (Losey and Denno, 1998, 1999; Snyder and Ives, 2003; Costamagna *et al*., 2007; Snyder, 2009; Grez *et al*., 2007, 2011, 2012; Vanacloacha *et al*., 2013; Kumar *et al*., 2014). However, in all such studies the coccinellids were reared under optimal prey conditions prior to being used for experimentation. Further, the evaluation of prey resource fluctuation in coccinellids is simply restricted to their predation and oviposition behaviour (Dixon and Guo, 1993; Schellhorn and Andow, 1999; Wagner *et al*., 1999; Snyder *et al*., 2000; Schüder *et al*., 2004; Phoofolo *et al*., 2007; Dmitriew and Rowe, 2007; Dmitriew *et al*., 2009; Chaudhary *et al*., 2016). And studies comparing the functional responses of coccinellids under prey fluctuation conditions are hardly investigated, despite the important role of predation in shaping community structure (Hiltunen and Laakso, 2013) and the major role of prey density in influencing rate of resource utilization by predators (Ives *et al*., 1993; Francis *et al*., 2000; Lee and Kang, 2004; Seagraves, 2009).

In the present study, we evaluated the functional response of the 4th instar larvae of *Menochilus sexmaculatus* (Fabricius) on two prey species, *viz*. cowpea aphid, *Aphis craccivora* Koch and mustard aphid, *Lipaphis erysimi* (Kaltenbach). *M. sexmaculatus* is a small-sized aphidophagous coccinellid of Oriental region that has wide prey range and greater competitive reproductive ability (Agarwala and Yasuda, 2000; Omkar *et al*., 2005). While *A. craccivora* has previously been reported a highly suitable prey for this coccinellid species, but being an aposematic prey, *L. erysimi* has reduced suitability for *M. sexmaculatus* due to presence of allyl isothiocyanates (Kumar *et al*., 2013). In this study, we abruptly changed the predators from their rearing condition of scarce, optimal or abundant prey supply to five different experimental conditions (extremely scarce, scarce, sub-optimal, optimal or abundant prey biomass) and observed their functional responses.

We hypothesized that although predators would exhibit type-II functional response curves, but predators reared on optimal or abundant prey would have better predation rates and higher functional response curves than those reared on scarce prey. Moreover, considering the fact that insect predators often make decision to consume toxic and well defended prey based on trade-off between benefits of gaining nutrients and energy with costs of ingesting toxins (Skelhorn and Rowe, 2006; Skelhorn *et al*., 2016), it was further hypothesized that slopes of functional response curves of *M. sexmaculatus* would be lower on *L. erysimi* than on *A. craccivora*. Thus, the study would not only provide information on behaviour of concerned predator in relation to its feeding, but would also help in assessing its energy budget for various biological activities. The study would also facilitate mass multiplication of this coccinellid species for augmentative biocontrol of aphid pests.

2 MATERIALS AND METHODS

2.1 Stock maintenance

Adult males and females (n = 100) of *M. sexmaculatus* were collected from the agricultural fields close to Varanasi, India (25°20′N, 83°0′E), paired and reared in plastic Petri dishes (14.5 cm × 1.5 cm) under constant abiotic conditions (27 ± 2℃ temperature; 65% ± 5% relative humidity; 14L∶10D photoperiod) in BOD Incubator (NSW-152; Narang Scientific Works Pvt. Ltd., New Delhi, India). They were segregated into two groups: one group was provided with *ad libitum* supply of intermediate instar larvae of *A. craccivora* raised on cowpea, *Dolichos lablab* L. (Fabaceae), while the other group was reared on *ad libitum* supply of intermediate instar larvae of *L. erysimi* raised on mustard, *Brassica campestris* L. (Brassicaceae). The eggs laid were collected every 24 h and observed for hatching. The neonates obtained were used for further experimentation.

2.2 Experimental design

Our experiments were divided into two parts. The first part considered optimization of different prey conditions for life stages of *M. sexmaculatus*, as suggested earlier (Chaudhary *et al*., 2016). The second part of experiment was performed to evaluate functional response of the 4th instar larvae under five prey biomasses (extremely scarce, scarce, sub-optimal, optimal or abundant).

2.2.1 Optimization experiment: Neonates were taken from the two different groups (mentioned earlier) and reared individually on *ad libitum* supply of their respective prey species till the 4th instar larval stage. Since the nymphal stages of both aphid species show size similarity (personnel observations). Hence, individual 4th instar larvae of the predator were provided prey biomass ranging from 1 to 20 mg, *i. e*., 1 mg (~2 aphids), 2 mg (~4 aphids), 5 mg (~10 aphids), 10 mg (~20 aphids), 15 mg (~30 aphids) and 20 mg (40 aphids) intermediate instar larvae of *A. craccivora* and *L. erysimi* for 24 h in ten replicates (biomass measured using Analytical Balance: RA-200, Roy Electronics, Varanasi, India). When there were no aphids left and the larvae survived, the minimum prey biomass was referred to as scarce condition. When aphids left were 1.00 ± 0.50 mg and larvae survived, the minimum prey biomass was referred to as optimal condition. When aphids left were 4.00 ± 1.00 mg, the minimum prey biomass was referred to as abundant condition. Scarce, optimal and abundant biomasses on both prey species were 2, 10 and 15 mg of aphids per larva per day, respectively. Moreover, 1 and 5 mg of aphids per larva per day were considered extremely scarce and sub-optimal biomasses, respectively.

2.2.2 Evaluation of functional responses: The 1st instar larvae of *M. sexmaculatus* (n = 60) were individually reared under scarce, optimal and abundant prey supply up to the 3rd instar larval stage under abiotic conditions similar to that of stock culture. After larvae moulted to the 4th instars, they were weighed prior to the experiment. Mortality of larvae was observed under scarce prey supply, *i. e.*, 20 and 35 larvae of *M. sexmaculatus* died prior to reaching the 4th instar larval stage when 60 1st instar larvae were reared on scarce conditions of *A. craccivora* and *L. erysimi*, respectively. Thus, more 1st instar larvae were added to the experimental setup from the stock culture to equalize the sample size.

The 4th instar larvae from each prey supply per prey species were divided into five groups of 10 each, giving a total of 300 4th instar larvae. They were kept singly in Petri dishes (size mentioned above) and provided with the 2nd/3rd instar larvae of *A. craccivora* or *L. erysimi* at different rates, *i. e.*, (i) extremely scarce supply of prey (1 mg), (ii) scarce supply (2 mg), (iii) sub-optimal supply (5 mg), (iv) optimal supply (10 mg), or (v) abundant supply (15 mg) for the next 24 h and kept in the above mentioned abiotic conditions. After 24 h, larvae and prey left in each Petri dish were weighed. Thereafter, the food of the larvae was switched back to their respective rearing conditions.

The natural reduction in aphid biomass in the absence of predators, if any, was analyzed by keeping 1, 2, 5, 10 and 15 mg of aphids per prey species, in five replicates each, under similar abiotic conditions for 24 h and reweighed. Thus, the average loss in aphid biomass in absence of predators, if any, was determined, which was deducted from the aphid biomass loss with presence of predator for 24 h to obtain the actual consumption rate of the predator.

2.3 Statistical analysis

The distributions of results in all data sets obtained in this study were checked for normality using the Kolmogorov-Smirnoff test. Means were separated using Tukey's test when data were normally distributed and variances were homogeneous (Bartlett's test for equal variances).

Analyses of functional responses recorded involved determining the type of functional response and estimating parameters of functional response curves (Juliano, 2001). Initially, to discriminate between Type-II and Type-III responses, the shape of functional response curve was analyzed using a logistic regression (Juliano, 2001) of the proportion of prey consumed (N_e) as a function of initial prey biomass (N_o). The data were fitted to a polynomial regression function using statistical software SAS (Version 9.0). The equation used was:

$$\frac{N_e}{N_o} = \frac{\exp\left(P_o + \mathrm{P}_1 N_o + \mathrm{P}_2 N_o^2 + \mathrm{P}_3 N_o^3\right)}{1 + \exp\left(P_o + \mathrm{P}_1 N_o + \mathrm{P}_2 N_o^2 + \mathrm{P}_3 N_o^3\right)} \qquad (1)$$

where, P_o (intercept), P_1 (linear), P_2 (quadratic) and P_3 (cubic) are the parameters to be estimated. Positive linear ($\mathrm{P}_1 > 0$) and negative quadratic ($\mathrm{P}_2 < 0$) parameters indicate a Type-Ⅲ functional response. If $\mathrm{P}_1 < 0$, proportion of prey consumed declines monotonically with the initial number of prey offered, thus describing a Type-Ⅱ functional response (Juliano, 2001). The Proc CATMOD procedure was used to estimate these parameters. The second analysis used a nonlinear least squares regression, Proc NLIN (SAS Version 9.0), to estimate parameter values (T_h and either 'a' for Type-Ⅱ, or 'b', 'c' and 'd' for Type-Ⅲ). Because the experiment was carried out without replacing the prey that were consumed, the appropriate model for a Type-Ⅱ functional response is 'random-predator' equation (Rogers, 1972):

$$N_e = N_o\{1 - \exp[a(T_h N_e - T)]\} \text{ – Type-Ⅱ} \qquad (2)$$

For modeling the type-III response, attack rate (a) in equation 3 was set in equation 2 as a function of prey density (Hassell, 1978). In the simplest generalized form, attack rate (equation 3) is a function of initial number of prey:

$$a = \frac{\mathrm{d} + \mathrm{b}\, N_o}{1 + \mathrm{c}\, N_o} \qquad (3)$$

in which b, c and d are constants that must be estimated. The simplest form arises when a is a function of initial density, as in equation 4.

$$N_e = N_o\{1 - exp[(\mathrm{d} + \mathrm{b}\, N_o)(T_h N_e - T)/(1 + \mathrm{c}N_o)]\} \text{ – Type-Ⅲ} \qquad (4)$$

where, N_e is the number of prey consumed, N_o is initial prey biomass, a is the attack rate, T_h is the handling time per prey, T is the total time of exposure, and b, c and d are constants. The parameters T_h and a in this case were also obtained using equation 2.

Data on prey consumption and the proportion of prey consumption by different predators when supplied with different biomasses of prey were subjected to general MANOVA with prey species (*A. craccivora* or *L. erysimi*), rearing conditions (scarce/optimal/abundant), experimental conditions (extremely scarce, scarce, sub-optimal, optimal and abundant) and their interaction as independent factors and prey consumption and proportion of prey consumption as dependent factors, followed by Tukey's *post hoc* comparison of means. Statistical analyses were performed using SAS (Version 9.0) and MINITAB 16.

3 RESULTS

The consumption of *A. craccivora* by the 4th instar larvae of *M. sexmaculatus* increased under scarce, optimal and abundant prey rearing conditions when the biomass of prey provided under experimental conditions was increased from extremely scarce (1 mg) to abundant (15 mg) (Table 1). In contrast, proportion of prey biomass consumed (N_e/N_o) by larvae decreased under the three rearing conditions when provided prey biomass was increased from extremely scarce to abundant. This decrease in proportion of prey biomass consumed by the 4th instars larvae when biomass of prey provided was increased indicates a type-II functional response. The results of maximum likelihood analyses of the data further confirmed this for the 4th instar larvae of *M. sexmaculatus* on *A. craccivora* under scarce, optimal and abundant prey rearing conditions (Table 2). By plotting a type-II functional response and fitting polynomial logistic regression models to the biomass and proportions of prey consumed, respectively, the resulting regression lines fitted the data well (Figs. 1 and 2).

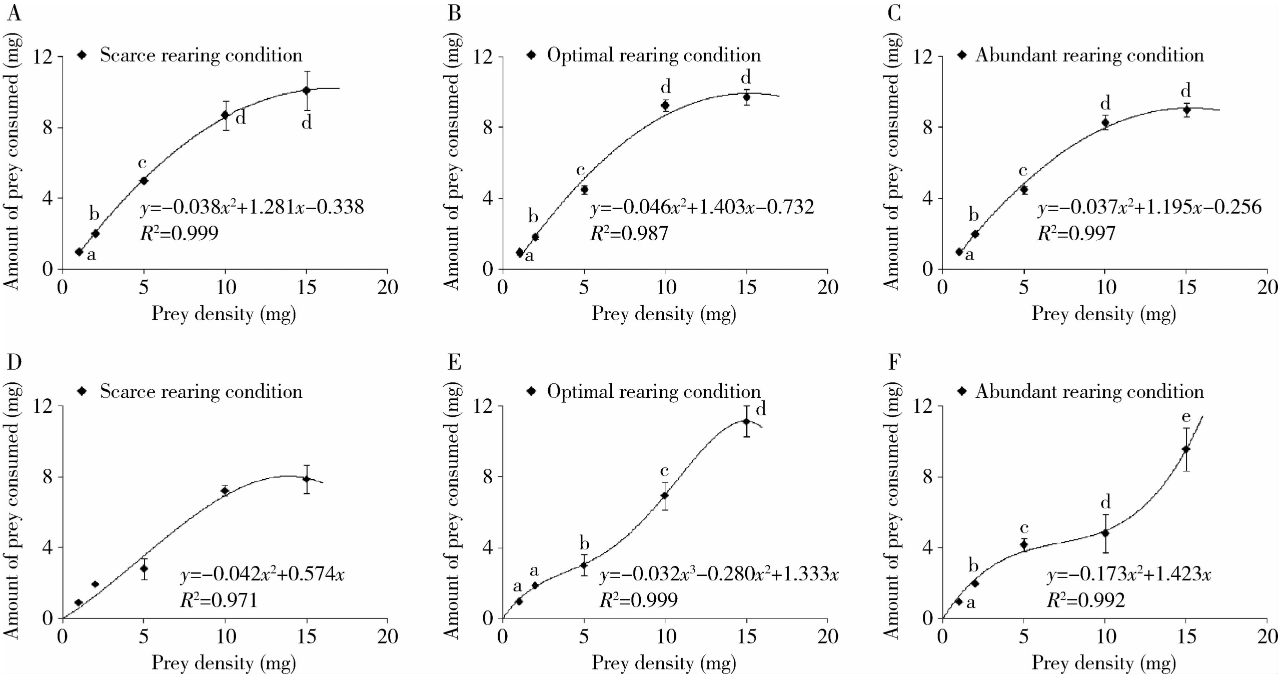

Fig. 1 Fitted relationships for the amount of prey consumed by the 4th instar larvae of *Menochilus sexmaculatus* when provided with five different biomasses of *Aphis craccivora* (A-C) and *Lipaphis erysimi* (D-F) as aphid species

Small letters represent comparison of means ± *SE* between the five prey biomasses (Tukey's *post hoc* comparison of means at $P < 0.05$ significance level).

Although the consumption of *L. erysimi* by the 4th instar larvae of *M. sexmaculatus* increased under the three rearing conditions when the biomass of prey provided under the experimental conditions was increased from extremely scarce to abundant. However, the curves of proportion of prey consumed on *L. erysimi* under scarce, optimal and abundant prey rearing conditions initially decreased (as in type-II) as the biomass of aphids provided increased from extremely scarce to sub-optimal/optimal, but subsequently increased (as in type-III) when food supply was increased from sub-optimal/optimal to optimal/abundant (Figs. 1 and 2). Further, the recorded significantly negative P_1 parameters suggested

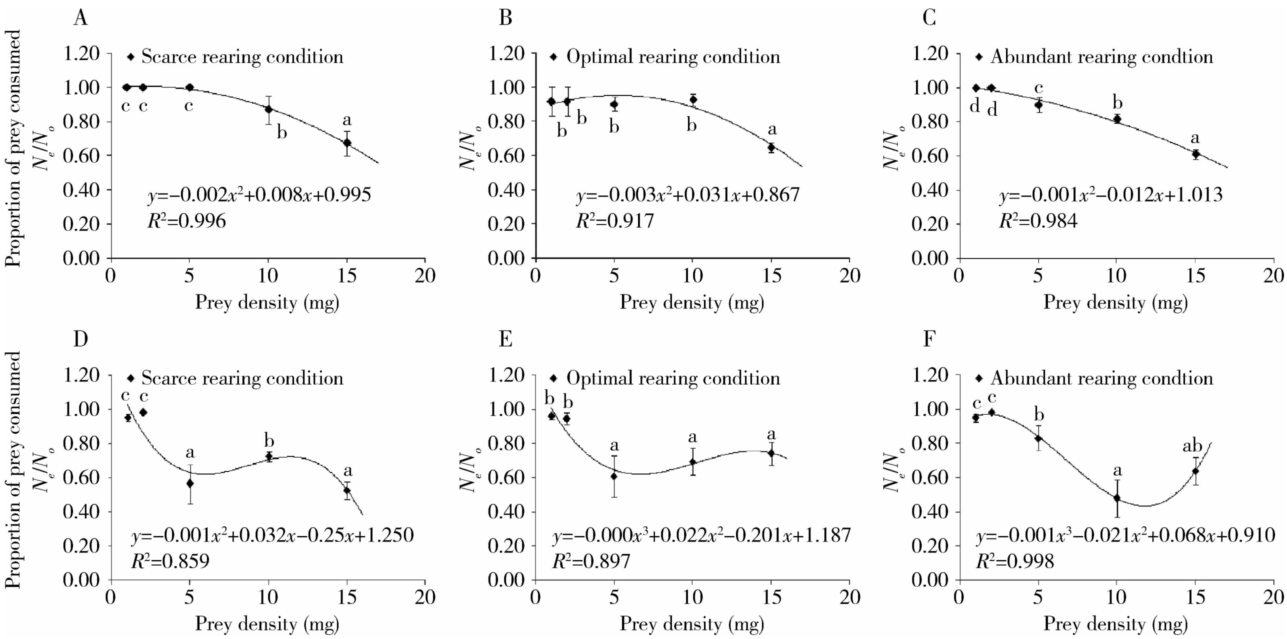

Fig. 2 Fitted relationships for the proportion of prey consumed (N_e/N_o) by the 4th instar larvae of *Menochilus sexmaculatus* when provided with five different biomasses of *Aphis craccivora* (A–C) and *Lipaphis erysimi* (D–F) as aphid species

Small letters represent comparison of means ± *SE* between the five prey biomasses (Tukey's *post hoc* comparison of means at $P < 0.05$ significance level).

Table 1 Prey consumption by the 4th instar larvae of *Menochilus sexmaculatus* when fed on *Aphis craccivora* and *Lipaphis erysimi*

Rearing prey conditions	Experimental prey conditions	Prey consumption (mg/d)	
		A. craccivora	*L. erysimi*
Scarce prey	Extremely scarce	1.00 ± 0.00 aA(a)	1.00 ± 0.00 aA(a)
	Scarce	2.00 ± 0.00 bA(a)	2.00 ± 0.00 bA(a)
	Sub-optimal	5.00 ± 0.00 cA(b)	2.83 ± 0.57 cA(a)
	Optimal	8.69 ± 0.84 dA(b)	7.24 ± 0.29 dA(a)
	Abundant	10.09 ± 1.11 dA(b)	7.89 ± 0.78 dA(a)
Optimal prey	Extremely scarce	0.92 ± 0.08 aA(a)	1.00 ± 0.00 aA(a)
	Scarce	1.83 ± 0.17 bA(a)	2.00 ± 0.00 bA(a)
	Sub-optimal	4.51 ± 0.21 cA(a)	4.61 ± 0.38 cA(a)
	Optimal	7.24 ± 0.34 dA(a)	6.99 ± 0.80 dA(a)
	Abundant	9.73 ± 0.44 eA(a)	11.16 ± 1.04 eA(a)
Abundant prey	Extremely scarce	1.00 ± 0.00 aA(a)	1.00 ± 0.00 aA(a)
	Scarce	2.00 ± 0.00 bA(a)	2.00 ± 0.00 bA(a)
	Sub-optimal	4.50 ± 0.21 cA(a)	4.33 ± 0.38 cA(a)
	Optimal	8.19 ± 0.27 dA(b)	4.82 ± 1.09 cA(a)
	Abundant	9.15 ± 0.41 eA(a)	9.57 ± 1.23 dAB(a)
Prey species (*Sp*)		$F = 10.63$; $df = 1, 299$; $P = 0.0010$	
Rearing prey condition (*R*)		$F = 2.94$; $df = 2, 299$; $P = 0.0550$	
Experimental prey condition (*T*)		$F = 287.71$; $df = 4, 299$; $P < 0.0001$	
Interaction ($Sp \times R \times T$)		$F = 2.06$; $df = 8, 299$; $P = 0.0400$	

Values are mean ± *SE*. Small and large letters represent comparison of means amongst experimental prey and rearing prey conditions, respectively; small letters in parentheses represent comparison of means between prey species.

the slopes of functional response curves to be declining, which is the characteristic of a type-II functional response (Table 2). Thus, the 4th instar larvae of *M. sexmaculatus* exhibited a modified type-II functional response on *L. erysimi*.

Table 2 Maximum likelihood estimates derived from the logistic regression of proportion of prey consumed as a function of the initial prey density by the 4th instar larvae of *Menochilus sexmaculatus* on *Aphis craccivora* and *Lipaphis erysimi*

Prey species	Rearing conditions	Parameters	Estimates	*SE*	χ^2-value	*P*-value
A. craccivora	** Scarce	Intercept (P_o)	3.6147	2.3285	2.41	0.1206
		Linear (P_1)	−0.0426	1.1027	0.00	0.9692
		Quadratic (P_2)	−0.00937	0.1412	0.00	0.9471
		Cubic (P_3)	0.000019	0.00520	0.00	0.9971
	** Optimal	Intercept (P_o)	3.9345	2.3602	2.78	0.0955
		Linear (P_1)	−0.3445	1.1236	0.09	0.7591
		Quadratic (P_2)	0.0540	0.1452	0.14	0.7102
		Cubic (P_3)	−0.00306	0.00539	0.32	0.5704
	** Abundant	Intercept (P_o)	4.5200	2.3009	3.86	0.0495
		Linear (P_1)	−0.7276	0.9771	0.55	0.4565
		Quadratic (P_2)	0.0612	0.1187	0.32	0.5714
		Cubic (P_3)	−0.00246	0.00426	0.33	0.5640
L. erysimi	** Scarce	Intercept (P_o)	7.0498	2.2203	10.08	0.0015
		Linear (P_1)	−2.6894	0.8759	9.43	0.0021
		Quadratic (P_2)	0.3272	0.1020	10.30	0.0013
		Cubic (P_3)	−0.0119	0.00358	11.10	0.0009
	** Optimal	Intercept (P_o)	5.7014	1.8480	9.52	0.0020
		Linear (P_1)	−1.9940	0.7492	7.08	0.0078
		Quadratic (P_2)	0.2272	0.0890	6.52	0.0107
		Cubic (P_3)	−0.00766	0.00317	5.85	0.0156
	** Abundant	Intercept (P_o)	2.9084	1.5618	3.47	0.0626
		Linear (P_1)	−0.0533	0.6832	0.01	0.9378
		Quadratic (P_2)	−0.0602	0.0846	0.51	0.4768
		Cubic (P_3)	0.00355	0.00307	1.34	0.2469

** A significant negative estimate for parameter P_1 indicates that the slope of the functional response curve is declining, which indicates a type-II functional response.

General MANOVA further revealed significant effect of prey species (*A. craccivora* or *L. erysimi*), experimental conditions (extremely scarce, scarce, sub-optimal, optimal and abundant) and interaction between the three independent factors on the amount of prey consumed (Table 1), and those of prey species (F = 18.24; df = 1, 299; $P < 0.0001$) and experimental conditions (F = 314.88; df = 4, 299; $P < 0.0001$) on the proportion of prey consumed (N_e/N_o) by predators. However, rearing conditions did not significantly affect the amount of prey consumed (Table 1). Moreover, neither the rearing conditions (F = 1.63; df = 2, 299; P = 0.1970) nor the interaction between three independent factors (F = 1.85; df = 8, 299; P = 0.0690) influenced the proportion of prey consumed.

Thus, on the three rearing conditions, the amount and proportion of prey consumed by the 4th instar larvae of *M. sexmaculatus* were similar when they were abruptly switched over to five different experimental conditions. Further, irrespective of rearing conditions, the 4th instar larvae showed the highest prey consumption on abundant prey and the lowest on extremely-scarce prey experimental conditions (Table 1; Fig. 1). In contrast, proportions of prey consumed by the 4th instar larvae were the highest on extremely scarce/scarce prey and the lowest on optimal/abundant prey experimental conditions (Fig. 2). Moreover, on the two prey species, both the amount and proportion of prey consumed were relatively higher on *A. craccivora* than on *L. erysimi* (Table 1; Figs. 1 and 2).

Results further revealed that the larval attack rate (a) was higher on *A. craccivora* than on *L. erysimi*; being the highest under optimal prey rearing condition (0.2484 ± 0.2432). In contrast, the prey handling time (T_h) was relatively higher on *L. erysimi* than on *A. craccivora*; being the highest under scarce prey rearing condition (2.6547 ± 0.2319) (Table 3).

Table 3 Estimates (± *SE*) of the attack rate (a) and handling time (T_h) plus the 95% confidence limits (CL) for the 4th instar larvae of *Menochilus sexmaculatus* derived from their functional responses when fed on *Aphis craccivora* and *Lipaphis erysimi*

Prey species	Rearing conditions	Attack rate (a)	95% CL		Handling time (h) (T_h)	95% CL	
			Lower	Upper		Lower	Upper
A. craccivora	Scarce	0.0639 ± 0.0372 aB	−0.0109	0.1387	2.1685 ± 0.1466 aA	1.8738	2.4633
	Optimal	0.2484 ± 0.2432 bB	−0.2405	0.7373	2.4197 ± 0.0776 bB	2.2636	2.5757
	Abundant	0.0528 ± 0.0133 aB	0.0259	0.0796	2.5098 ± 0.0821 bA	2.3447	2.6748
L. erysimi	Scarce	0.0194 ± 0.0062 bA	0.0069	0.0318	2.6547 ± 0.2319 bB	2.1884	3.1210
	Optimal	0.0098 ± 0.0032 aA	0.0034	0.0162	1.3766 ± 0.3586 aA	0.6556	2.0976
	Abundant	0.0103 ± 0.0046 aA	0.0009	0.0195	2.0666 ± 0.4643 abA	1.1331	3.0002

Values are mean ± *SE*. Small and large letters represent comparison of means amongst rearing conditions and between prey species, respectively.

4 DISCUSSION

In the present study, the 4th instar larvae of *M. sexmaculatus* exhibited Type-II functional response when reared on scarce, optimal or abundant supply of *A. craccivora* but tested on five experimental conditions of the same prey species. Such response is characterized by a curvilinear increase in predation with increase in prey density, becoming asymptotic at high prey densities and thereafter remaining constant due to satiation (Mills, 1982; Jalali *et al.*, 2010). Similar results with a Type-II functional response in coccinellids have also been reported earlier (Bayoumy, 2011a, 2011b; Omkar and Pervez, 2011; Osman and Bayoumy, 2011; Gupta *et al.*, 2012; Omkar and Kumar, 2013; Kumar *et al.*, 2014; Chaudhary *et al.*, 2015).

In contrast, the 4th instar larvae showed modified type-II functional response under the three rearing and five testing conditions of *L. erysimi*. These results may be owing to the small size of experimental arena (Petri dishes). Similar unusual results have also been reported earlier for the parasitoid, *Aphytis diaspidis* Howard (Bayoumy, 2011b) and coccinellid predators, *Stethorus gilvifrons* Mulsant (Osman and Bayoumy, 2011) and *M. sexmaculatus* females (Chaudhary *et al.*, 2015). Kumar *et al.* (2014) also reported modified Type-II functional response curves when *Coccinella septempunctata* (L.) and *Coccinella transversalis* F. were kept in conspecific and heterospecific combinations and exposed to increasing biomass of pea aphid.

In the present study, irrespective of the rearing conditions, the 4th instar larvae of *M. sexmaculatus* showed the highest prey consumption on abundant prey and the lowest on extremely scarce prey experimental conditions. It is assumed that when abundant prey is available for feeding, larvae consume maximum prey biomass to enhance their growth and complete their development earlier than the larvae feeding on low prey biomass. However, low prey availability retards the consumption rates of the 4th instar larvae because sufficient prey biomass is not available for feeding. In contrast, the proportions of prey consumed by the 4th instar larvae were the highest on low prey biomass and the lowest on high prey biomass. Such findings further substantiate that predators feeding on high prey biomass get satiated earlier than those feeding on low prey biomass. The present findings are in agreement with those reported earlier in coccinellids (Schüder *et al.*, 2004; Agarwala *et al.*, 2008; Atlihan and Guldal, 2009; Omkar *et al.*, 2010; Maurice and Ashwani, 2011; Kumar *et al.*, 2014; Chaudhary *et al.*, 2015).

Moreover, no significant effect of rearing conditions on the consumption rates of the 4th instar larvae were recorded in the present study. The results, thus, corroborate that despite having sub-optimal consumption rates on scarce prey rearing condition, larvae of *M. sexmaculatus* possibly compensate for a shortage of food by converting and using higher prey biomass than usual when suddenly meet optimal or abundant prey experimental conditions. There are also possibilities that the predators may have increased their conversion efficiencies and growth rates under scarce prey rearing condition, since these are amongst the several mechanisms displayed by coccinellids to overcome the shortage of trophic resource, as reported earlier by Schüder *et al.* (2004) in the larvae of *Adalia bipunctata* and Chaudhary *et al.* (2016) in larvae and adults of *M. sexmaculatus* and *P. dissecta*.

In the present study, both the amount and proportion of prey consumed were relatively higher on *A. craccivora* than on *L. erysimi*. Moreover, larval attack rates (*a*) were recorded higher and their prey handling time were lower on *A. craccivora* rather than on *L. erysimi*. These results further substantiated that differential biomass consumption and utilization is perhaps indicative of aphid palatability and of a coccinellid's preference for a particular species of aphid prey of suitable morphology, behaviour and chemical constitution (Okamoto, 1966; Dixon, 2000). It is supposed that the allelochemicals that *L. erysimi* derives from its host plants are less suitable for the metabolic activity of *M. sexmaculatus*. In contrast, the better performance of *M. sexmaculatus* when fed on *A. craccivora* may be attributed to the presence of suitable nutrients in this aphid species which they derive from their host plant (Rajmohan and Jayraj, 1974; Islam and Haque, 1978; Omkar *et al.*, 2005), *i. e.*, *Dolichos lablab*. Earlier studies have also reported the high suitability and palatability of *A. craccivora* to *M. sexmaculatus* when reared on the same host plant (Omkar and Bind, 2004).

In summary: (i) Despite prey resource fluctuations, the 4th instar larvae exhibited type-II response on *A. craccivora* but a modified type-II response on *L. erysimi*, *i. e.*, fluctuations in defended prey availability altered functional response curves of the 4th instar larvae. (ii) Irrespective of prey species, the 4th instar larvae that were reared on optimal/abundant prey exhibited normal predation rates on five experimental conditions. But, the 4th instar larvae reared on scarce prey compensated for a shortage of food by consuming higher prey biomass than usual when suddenly switched over to optimal/abundant prey experimental conditions. (iii) But they exhibited the highest prey consumption on abundant prey and the lowest on extremely scarce prey experimental conditions. (iv) Moreover, higher attack rate but lower prey handling time on *A. craccivora* suggests its higher suitability as a prey for *M. sexmaculatus* than *L. erysimi*. However, field based studies are still needed to strengthen present findings.

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防御性被捕食者可利用量的波动可调节六斑月瓢虫的功能反应曲线

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摘要:【目的】本研究评价了在被捕食者波动条件下,在花生蚜 *Aphis craccivora* Koch 和萝卜蚜 *Lipaphis erysimi* (Kaltenbach)上六斑月瓢虫 *Menochilus sexmaculatus* (Fabricius)4 龄幼虫的功能反应。萝卜蚜是一种含烯丙基异硫氰酸酯的防御性被捕食者。我们推测,在试验的被捕食者条件下,在最适量被捕食者或丰富的被捕食者条件下饲养的幼虫比在缺乏被捕食者条件下饲养的幼虫表现出更好的功能反应。而在萝卜蚜上六斑月瓢虫的功能反应曲线的斜率比在花生蚜上要低。【方法】将六斑月瓢虫 4 龄幼虫从饲养条件(缺乏被捕食者/最适乏被捕食者/丰富的被捕食者)突然转移到不同的试验条件(极为缺乏被捕食者/缺乏被捕食者/次适量被捕食者/最适量被捕食者/丰富的被捕食者)下,外推出其功能曲线。【结果】尽管被捕食资源发生了改变,但是六斑月瓢虫 4 龄幼虫在花生蚜上表现出Ⅱ型反应,而在萝卜蚜上表现出改变的Ⅱ型反应。此外,在 5 个试验条件下,不管是哪种被捕食者,在最适量被捕食者/丰富的被捕食者条件下饲养的 4 龄幼虫均表现出正常的捕食率。但是在缺乏被捕食者条件下饲养的 4 龄幼虫突然转变到最适量/丰富的被捕食者实验条件下时,它们通过取食比平时更多的被捕食者的生物量来补偿食物的短缺。不过,它们在丰富的被捕食者条件下的取食量最高,在极为缺乏被捕食者的试验条件下的取食量最低。而且,在花生蚜上记录到较高的攻击率和较低的猎物处理时间。【结论】结果说明,萝卜蚜可利用量的波动可改变六斑月瓢虫幼虫的功能反应。然而,对于六斑月瓢虫而言,花生蚜比萝卜蚜是更为合适的被捕食者。

关键词: 瓢虫; 蚜虫; 生物防治; 功能反应; 资源波动

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